Dispersal will limit ability of mammals to track climate change in the Western Hemisphere

Carrie A. Schloss[1], Tristan A. Nuñez, and Joshua J. Lawler

School of Environmental and Forest Sciences, University of Washington, Seattle, WA 98195

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As they have in response to past climatic changes, many species will shift their distributions in response to modern climate change. However, due to the unprecedented rapidity of projected climatic changes, some species may not be able to move their ranges fast enough to track shifts in suitable climates and associated habitats. Here, we investigate the ability of 493 mammals to keep pace with projected climatic changes in the Western Hemisphere. We modeled the velocities at which species will likely need to move to keep pace with projected changes in suitable climates. We compared these velocities with the velocities at which species are able to move as a function of dispersal distances and dispersal frequencies. Across the Western Hemisphere, on average, 9.2% of mammals at a given location will likely be unable to keep pace with climate change. In some places, up to 39% of mammals may be unable to track shifts in suitable climates. Eighty-seven percent of mammalian species are expected to experience reductions in range size and 20% of these range reductions will likely be due to limited dispersal abilities as opposed to reductions in the area of suitable climate. Because climate change will likely outpace the response capacity of many mammals, mammalian vulnerability to climate change may be more extensive than previously anticipated.

Recent changes in climate have already caused discernible shifts in species distributions (1, 2). In general, these shifts have been toward the poles or upwards in elevation and have occurred at an average rate of 6.1 km and 6.1 m per decade, respectively (3). Given the projected rates of future climatic changes, rates of range shifts over the coming century are likely to be even greater (4–6). Several studies have projected potential shifts in species distributions in response to forecasted climatic changes. Because these range-shift projections rarely account for dispersal abilities, they indicate areas that may be climatically suitable for species in the future, but they do not tell us whether species will be able to expand their ranges into these newly suitable regions.

In the coming century, the survival of species will in part depend on their abilities to track geographic changes in suitable climates (7, 8). This ability to keep pace with climate change depends on both the velocity of the climatic changes a species will face and species-specific dispersal abilities. Loarie et al. (8) mapped the velocity of climate change as the ratio of temporal and spatial gradients of changes in mean temperature, and separately, in annual precipitation. Temperature and precipitation are expected to change globally at average velocities of 0.42 and 0.22 km/y, respectively, and the velocities of changes in both of these climatic variables also vary spatially. The velocity of climate change that a species will face, or the velocity at which a species will need to move to keep pace with shifts in suitable climates, therefore, depends on the location of the species and the velocities of changes in the particular climatic factors that influence the species' distribution.

At broad spatial scales, species' distributions are largely determined by multiple, interacting, climatic factors (9). Bioclimatic models identify the relationship between species' distributions and climate and can be used to project the future locations of suitable climates (10, 11). The velocity at which a species will likely need to move from a given location to track these shifts in suitable climates can be measured as the distance from that location within the species' current range to the closest location projected to have a suitable climate in the future divided by the time period of the projected climatic changes. This species- and location-specific measure of the velocity of climate change will likely vary for different species at a single location and across different locations within the range of a single species.

The ability of species to keep pace with climate change also depends on species-specific dispersal abilities and the degree to which the landscape facilitates or impedes movement. Dispersal can be defined as the movement of an individual outside of its home range without anticipated return (12). Dispersal may occur before the first mating (natal dispersal) or between breeding seasons in adults (breeding dispersal). Dispersal velocity, or the distance that a given species can disperse over a given time period, depends on both the distance of individual dispersal events and the frequency of those events. In addition to dispersal ability, land use also affects species overall movement. Landscapes that do not provide suitable habitat for movement, survival, or reproduction reduce the abilities of species to track climatic changes.

We investigated the potential for mammals in the Western Hemisphere to keep pace with a changing climate by comparing the velocities of climate change that each of 493 mammals will likely experience with modeled dispersal velocities for these species. First, we calculated the velocity of climatic changes relevant to each species on a cell-by-cell basis across a 0.5° by 0.5° grid using bioclimatic model projections for the coming century. Next, we modeled dispersal velocities for each species as a function of body mass, diet type, the successive time between generations, and the potential variability in dispersal distances. We then determined the percentage of species in each grid cell for which the velocity of climate change will likely exceed the species' dispersal velocity, and thus, the percentage of species that will be unable to keep pace with projected climate changes. We also investigated the relative degree to which human land use may further impede movement of species by analyzing land-use patterns along simple movement routes connecting current and future suitable climates and calculated the additional distances that some species may need to travel to avoid movement through less suitable landscapes.

Results

On average, across the Western Hemisphere and 10 projected future climates, 9.2% of the mammals in a given grid cell will likely be unable to keep pace with the changing climate (Fig. 1). In some areas, up to 39% of the mammals will be unable to track climate change. Furthermore, projections from three of the climate models indicate that over 50% of the mammals in given

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[1]To whom correspondence should be addressed. E-mail: cschloss@u.washington.edu.

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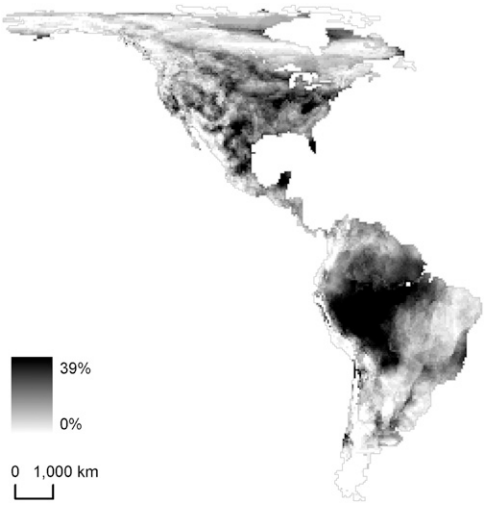

Fig. 1. Percentage of mammalian species that are projected to be unable to keep pace with climate change. Results are average percentages across projections that incorporate the output from 10 climate models run for a midhigh (SRES A2) emissions scenario.

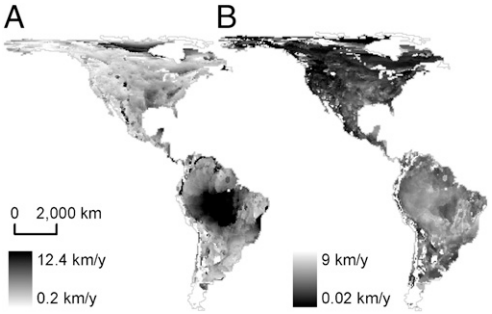

Fig. 2. Average velocity of climate change as projected by 10 climate models (*A*) and average dispersal velocity (*B*) of all mammals that are projected to be unable to keep pace with climate change.

locations will be unable to keep pace with climate change (*SI Appendix*). Species will be least likely to be able to track climatic changes in the tropical and subtropical moist broadleaf forest biome of the western Amazon. In this biome, on average, 14.5% of species will likely be unable to keep pace with climate change.

The inability of mammals to track climate change will be driven more by rapid climatic changes in some regions (Fig. 2*A*) and more by limited dispersal abilities in others (Fig. 2*B*). In the Amazon, the Yucatan Peninsula, the Appalachian Mountains, and the south–central United States, the subset of species that will likely be unable to reach suitable climates will experience high velocities of climate change. For example, in some locations in the Amazon, the average dispersal velocity for this subset of species is about 1 km/y, but the average velocity of climate change experienced by this subset of species can be as high as 8 km/y. In contrast, the subset of species that will likely be unable to track their climatic niches in western Mexico and the Midwest and western United States are more limited by dispersal ability. The average dispersal velocity for these species is only 0.1–0.5 km/y. Thus, despite the relatively low velocities of climate change projected for these species (about 1 km/y), even lower dispersal velocities will likely prevent them from tracking climate change.

Our results indicate that primates and eulipotyphla (shrews and moles) will be the mammalian taxa least able to keep pace with climate change and carnivora, artiodactyla (even-toed ungulates), and xenarthra (armadillos, anteaters, and sloths) will be the most able to keep pace (Fig. 3*A*). We exclude the order microbiotheria in the taxonomic evaluation of the results because the Monito del Monte (*Dromiciops gliroides*) is the only species in this order. The primates are more dispersal limited than the other orders and many primates may need to expand their ranges over longer distances than species of other orders to reach suitable climates (Fig. 3*B*). In contrast, the orders carnivora and artiodactyla are the least-dispersal limited and the distances they need to disperse are short, relative to the distances required of species of other orders.

On average, across all 10 climate projections, 87% of mammals are expected to experience reductions in range size. Twenty percent of these reductions are due to dispersal limitations rather than a reduction in the area that is climatically suitable. The average projected change in range size is a reduction of 37%. Nearly all primates will experience severe reductions in range size. The average projected change in range size for species in the order primates is a reduction of 75%. Conversely, many species ranges in the orders carnivora and arctiodactyla may actually expand (Fig. 4).

In many places, land use will likely make it even more difficult for species to keep pace with climate change (Fig. 5). In the midwestern and Appalachian regions of the United States, movement of species, already dispersal limited, may be further constrained by the extensive human land use in these regions. Species in the Amazon region are limited by dispersal ability, but face lower intensities of human land use, except in a few regions in western Brazil. In contrast, in southeastern Brazil, movement of mammals may not be dispersal limited, but species will need to move through landscapes with high human impacts, and so, their movement may be inhibited or they will have to travel farther to avoid inhospitable landscapes. To avoid movement through human-dominated landscapes and large bodies of water, mammals will need to disperse an average of 0.8 km/y faster to reach suitable climate (based on a random subset of 38 mammals, *SI Appendix*). An additional 2.4% of species' ranges will be unable to keep pace with climate change as a result of these alternative dispersal routes (*SI Appendix*). The impact of the longer dispersal routes on species' abilities to track changes in climate will likely be greatest for primates and rodents (*SI Appendix*).

Discussion

Species vulnerability to climate change depends on exposure, sensitivity, and the capacity to respond to climatic changes (13). Although exposure to climate change is projected to be greatest at higher latitudes (14), our results indicate that most mammalian species at high latitudes will likely be able to keep pace with these large changes. The geographic differences between projected magnitudes of climate change and our results could be due to higher latitudinal gradients in climate or a greater capacity to respond to large climatic changes, given the greater dispersal abilities of some of the mammals in these regions. Conversely, in the tropics, many species lack the ability to keep pace with climate change despite forecasts for less dramatic changes in climate. Here, higher percentages of species unable to reach suitable climates may be the result of lower latitudinal gradients in climate in the tropics and/or higher sensitivity to climatic changes due to narrower climatic niches of tropical species. In tropical regions, species generally have more restricted physiological tolerances and hence are expected to be more sensitive to climate change (15, 16).

The orders primates and eulipotyphla are least able to keep pace with climate change and are the most likely to experience climate-change–induced range reductions. The primates are also currently the most threatened taxon in our study with 35% already classified as critically endangered, endangered, or vulnerable on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (17) and an additional

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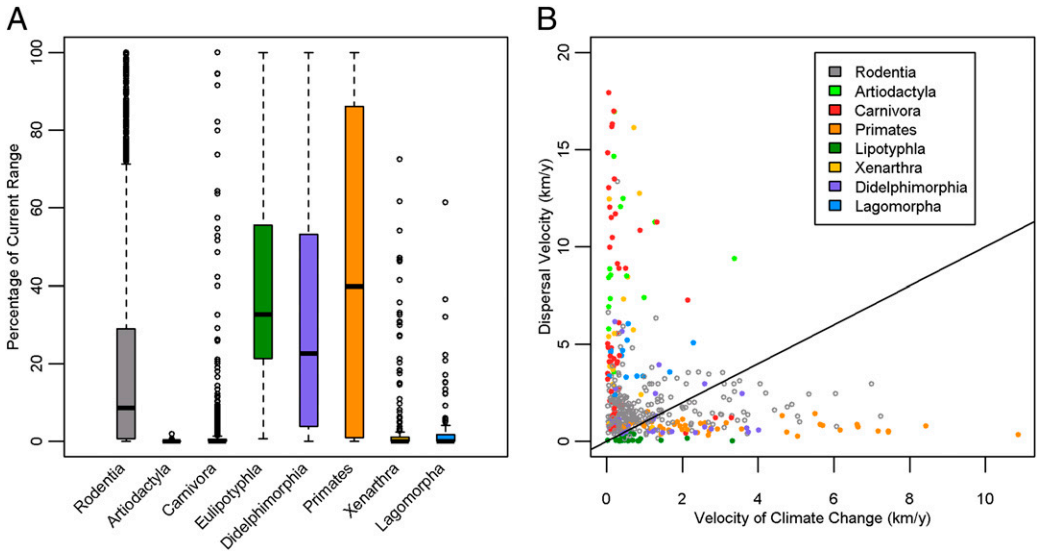

Fig. 3. Estimates of the ability of species in each order in the class mammalia to track projected climate change. (*A*) Percentage of grid cells in each species' range from which that species will likely be unable to track shifts in suitable climate. Boxplots incorporate percentages from each of 10 estimates based on the output from 10 climate models for each mammalian species. Boxes represent the interquartile range. Dashed whiskers extend to the lowest and highest values within 1.5 times the interquartile range. Values that are more extreme than the dashed whiskers are plotted as circles. (*B*) Modeled dispersal velocity plotted against the velocity (averaged across every grid cell in a species range and across projections from 10 climate models), at which each species will need to move to keep pace with climate change. Species that, on average, will likely be unable to keep pace with a changing climate fall below the solid line, whereas species that will likely be able to keep pace, on average, with a changing climate are above the solid line. Ten species of carnivora and three species of xenarthra with dispersal velocities greater than 20 km/y, but with velocities of climate change that were less than 2 km/y are not plotted here (n = 480).

29% listed as near threatened (*SI Appendix*). However, the IUCN Red List lists climate change as a threat for only one of these species, the black howler monkey (*Aluatta pigra*). Our results indicate that primates will be further threatened by climate change. Knowledge of the potential vulnerabilities of this order to climate change will enable management efforts to focus on species that are most vulnerable to climate change by minimizing the current threats to these species and fostering more resilient populations.

Landscape Permeability. We are underestimating the percentages of species that will be unable to keep pace with climate change because the percentages are based on dispersal estimates that do not incorporate landscape permeability. Landscape permeability is the degree to which the landscape facilitates animal movement (18). Human-dominated land uses between some species' ranges and regions of future suitable climate will increase the percentage of species that are unable to keep pace with climate change by requiring faster dispersal along longer alternative routes. In regions in which extensive human land use is ubiquitous, inhospitable landscapes may not lengthen dispersal routes because alternative routes through more permeable landscapes may not be available. In the subsample of 38 species, carnivores will likely travel through landscapes with extensive human land use, but those landscape patterns will have relatively little impact on their movement routes. In these regions and for these species, dispersal may be less successful due to the potential for decreased survival and reproduction in less suitable habitats. Fig. 5 is derived from straight-line movement routes of all 493 mammals and it highlights the regions from which we estimate land use to make keeping pace with climate change more difficult either as a result of increased distances in dispersal routes or decreased fitness. In eastern Brazil, the eastern United States, southern Mexico, and Central America, species are likely to reach suitable climate when the permeability of the landscape along the dispersal route is ignored. However, extensive human land use between these regions and regions of future suitable climate will likely add additional challenges to the capacity for species to track their climatic niches. These regions may therefore be important areas from which to focus connectivity efforts because in these regions species have the ability to keep pace with climate change, provided that the landscape does not impede their survival or movement. In addition to incorporating the human-dominated land uses into species' dispersal routes, incorporating species-specific habitat preferences along with projected changes in habitat through time would generate more realistic estimates of the velocities species need to travel to reach suitable climates. However, the detailed data required for these analyses are not available for most species and the extensive processing time required for least-cost modeling makes these analyses infeasible for large numbers of species.

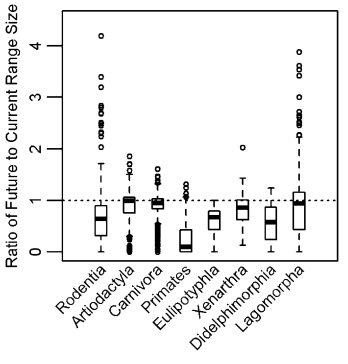

Fig. 4. The ratio of future projected range sizes (as limited by dispersal) to current range sizes. Boxplots incorporate ratios from projections based on each of 10 climate models individually for each mammalian species. Boxes represent the interquartile range. Dashed whiskers extend to the lowest and highest value within 1.5 times the interquartile range. Values that are more extreme than the dashed whiskers are plotted as circles. Values above the dashed line (i.e., ratios greater than one) indicate projected expansions in range size, whereas values below the dashed line (i.e., ratios less than one) indicate projected contractions in range size.

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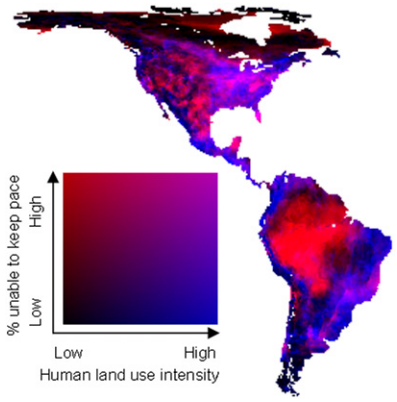

Fig. 5. Degree to which human land use may further impede movement of species attempting to track climate change. Red areas are highly vulnerable regions due to the inability of mammals to keep pace with climate change, but have relatively permeable landscapes. Blue areas are areas where species dispersal velocities and climate change velocities could allow them to keep pace with climate change; however, high intensities of human land use may prevent them from doing so. Pink areas highlight regions in which there are high percentages of species that, given their potential dispersal velocities and the velocities of climate change, will be unable to keep pace with climate change and from which dispersers will encounter human-dominated landscapes.

Dispersal Assumptions. Some of the assumptions we make in estimating dispersal likely result in underestimates of the percentages of mammals unable to reach suitable climate. For example, we assume that successful reproduction occurs at the youngest age biologically possible and that offspring in every generation survive to dispersal age and successfully disperse. In reality, dispersal has high associated mortality (12, 19). We also assume that suitable habitat and climates for establishment, survival, and reproduction will exist between regions of current and future climate and that individuals will disperse directly toward the closest suitable grid cell. However, smaller-bodied mammals generally have more tortuous or winding dispersal paths (20). More sinuous dispersal paths in smaller species that are, in general, already dispersal limited may further inhibit the ability for small species to keep pace with climate change. Finally, in our model, dispersal trajectories ignore topography, rivers, roads, and other dispersal barriers, which may either impede movement or increase travel distance by requiring animals to take alternate routes. Alternatively, we may overestimate the percentage of mammals unable to keep pace because reduced habitat suitability may lead to adaptation of increased dispersal distances (2, 21).

Although we may overestimate or underestimate dispersal velocities for particular species, in general, the overall patterns of our results are relatively insensitive to uncertainties in natal dispersal velocity. To investigate the impacts of these uncertainties, we applied our models using a range of dispersal velocity estimates that varied by more than 200 km/y for some species (*SI Appendix*). Using the different dispersal estimates resulted in no change in the relative patterns of geographic and taxonomic inabilities to keep pace with climate change and little change in the magnitude of the results (*SI Appendix*). For example, across 90% of the Western Hemisphere, using the lowest and highest estimates of dispersal velocity resulted in, at most, a difference of four mammals that could not keep pace with climate change. The largest difference was nine mammals and it only occurred in 0.013% of the grid cells of the Western Hemisphere.

Although taxonomic patterns are insensitive to natal dispersal estimates, the results are sensitive to dispersal frequency. For a subset of 193 species, a maximum estimate of breeding dispersal velocity that ignores the time between generations was relatively greater for species with delayed reproductive maturity such as ungulates, carnivores, and primates. These estimates had negligible impacts on the results for carnivores and ungulates, but resulted in a 52% average decrease in the percentage of primates' ranges that will be unable to keep pace with climate change (*SI Appendix*). However, this estimate represents the upper limit of species' movement potential rather than a likely dispersal scenario because natal dispersal is generally more common than breeding dispersal due to the evolution of a natal dispersal strategy (22) and is often the single largest long-distance movement event (12).

Suitable Climate Assumptions. In addition to potential errors in estimates of dispersal velocities, our estimates of the velocity of climate change may also be influenced by assumptions and uncertainties. Most notably, we used bioclimatic model projections to delineate future suitable climate, and so, we inherently incorporated some of the assumptions and uncertainties of bioclimatic modeling. These assumptions have been extensively reviewed elsewhere (10, 23) and can cause over- or underestimates in our results. For example, false assumptions of climatic intolerance due to modeling only the realized niche, and therefore ignoring species interactions and other nonclimatic determinants of range boundaries, may increase the projected distance a species needs to travel to suitable climate and cause overestimates of the percentages of species unable to track climate change (e.g., our results in southern Florida). In addition, correlative models have inherent uncertainties associated with their inability to project the suitability of novel climates and to account for evolution. Also, range expansions may occur from small populations that are already closer to regions of future suitable climate, but that are absent from our projections due to the coarse resolution of range maps (7). Conversely, the assumption that the climate throughout a species distribution is sufficient for persistence of all populations of that species will lead to underestimates of percentages of mammals unable to reach suitable climate because current distributions may not exist in equilibrium with current climate or species may be locally adapted to specific climates within their distributions. The bioclimatic model projections in our study also contain uncertainty because they are based only on climatic variables and derived from one type of bioclimatic model. Incorporating vegetation or soil types as predictor variables or using alternate bioclimatic models would likely result in different projections of species distributions and possibly in greater or lesser velocities of climate change (24, 25). Additionally, bioclimatic model projections contain inherent uncertainty due to their dependence on output from uncertain climate models (23). However, the patterns produced by our models are geographically and taxonomically very similar across the 10 climate-change scenarios used in our models (*SI Appendix*). Therefore, our geographic and taxonomic assessment of the ability of mammals to keep pace with climate change is somewhat insensitive to differences in climate model output.

Impact of Dispersal on Range-Shift Projections. Most previous range-shift projections have ignored dispersal. Our results indicate that species-specific dispersal is extremely important to include in range-shift projections. Assumptions of unlimited dispersal generally lead to overestimates of potential future range expansions and underestimates of potential range contractions. Our models indicate that 58% of range expansions projected with the assumption of unlimited dispersal will likely be range contractions when dispersal limitations are taken into account (*SI Appendix*). Furthermore, dispersal velocities vary by order and the failure to incorporate dispersal has more of an impact on the range-shift projections for species that are less able to expand into newly suitable climate such as primates and eulipotyphla (*SI Appendix*).

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Conclusions

Our study quantifies, over a large geographic area and for a large number of species, the ability of mammals to keep pace with climate change. We assessed the combined impact of the exposure and sensitivity of mammals to climate change in the Western Hemisphere and evaluated one aspect of the capacity of these mammals to respond. Despite uncertainties, incorporating dispersal into range-shift projections should greatly improve projections of species distributions and assessments of taxonomic and regional vulnerabilities, particularly for dispersal-limited species. Our results indicate that large percentages of mammals will likely be unable to keep pace with climate change in the Amazon and that primates will likely be some of the most vulnerable mammals. These results are robust to some of the uncertainties in climate change and in species' dispersal abilities.

For dispersal-limited species (e.g., primates, shrews, and moles), reducing nonclimatic stressors will help to foster more resilient populations (Table 1). Assisted colonization may also be an option for dispersal-limited species; however, there are many uncertainties and risks associated with such actions and detailed assessments are needed if these actions are to be considered (26). Our study highlights a number of species that may be candidates for assisted colonization and for which further research into the costs and benefits of these actions may be practical. Our results also highlight areas in which landscapes could be made more permeable to allow species to better track climate change. Conservation planners in these regions can focus on how land-use practices can facilitate climate-change–related dispersal and range expansions into regions of newly suitable climate. Although reducing other threats, intentionally moving species, and increasing the permeability of the landscape may help some species track climatic changes, ultimately reducing greenhouse gas emissions and thus reducing the velocity of climate change is the only certain method to ensure that many species will be able to keep pace with climate change.

Methods

Velocity of Climate Change. We calculated velocities of climate change (in kilometers per year) for each grid cell in each species' current range based on the distances between those grid cells and the closest grid cell projected to be climatically suitable for that species over an averaged 30-y period from 2071 to 2100. We divided this distance by 110 y—the difference between the historical time period (1961–1990) and the future time period on which the climate projections were based. We determined geographic distributions of future suitable climates for each species using existing bioclimatic model projections (6). Bioclimatic models use relationships between current species distributions and current climate variables in conjunction with projected future climatic data to forecast the locations where climate might be suitable for species in the future (10, 27). The bioclimatic models we used were based on random forest predictors (28, 29) and were built using current species distributions derived from digital range maps (30) and 37 different bioclimatic variables (6). Random forest models—a model-averaging approach based on classification or regression trees—have been shown to outperform other modeling approaches for predicting distributions of mammals in the Western Hemisphere (25). The models we used correctly predicted at least 80% of the presences and at least 97% of the absences in semi-independent test datasets that were reserved during the model-building process. We used projected future distributions of suitable climate for each mammal from these established relationships and climate projections from 10 general circulation models (*SI Appendix*) run for a midhigh [Special Report on Emissions Scenarios (SRES) A2] (31) greenhouse gas emissions scenario to calculate the velocity of climate change for each species. Although our projections are based on a midhigh emissions scenario, our results may be conservative because the emissions trajectory of the last decade has already exceeded the trajectory of this scenario (32).

Velocity of Dispersal. Of the 525 nonvolant mammals for which Lawler et al. built models (6), we obtained from the literature or estimated body masses, diet types, and generation lengths for 493 species (*SI Appendix*). We used this information to calculate dispersal velocity for 92 carnivores, 233 herbivores, and 168 omnivores. The velocity of dispersal (i.e., the distance that a species can travel over 110 y converted to velocity by dividing by that number of years) depends on the distance and frequency of dispersal events. We modeled the distances for single-natal dispersal events for each of the 493 species using the positive allometric relationships between median dispersal distances in kilometers (D) and body masses in kilograms (M) for carnivores and together for herbivores and omnivores (Eqs. **1** and **2**, respectively) and the probability of dispersing shorter or longer distances (d) relative to this median distance (Eq. **3**) (12).

$$D_{\text{Carn}} = 3.45 * M^{0.89} \quad [1]$$

$$D_{\text{HerbOmn}} = 1.45 * M^{0.54} \quad [2]$$

$$\Pr(d > D) = e^{-(D/1.5)} \quad [3]$$

Because natal dispersal occurs before the first reproductive event, we estimated the frequency of natal-dispersal events from the successive period between generations determined by gestation length, age at sexual maturity, and the period until the next breeding season. We determined total dispersal distances in 110 y by multiplying the distances of single natal-dispersal events by the number of potential dispersal events calculated by dividing 110 by the period between successive generations.

Table 1. Species- and region-specific examples of management strategies for climate-change adaptation

Velocity of climate change	Dispersal velocity	Human land use	Example order/region	Vulnerability to climate change	Conservation action
High	Low	High	Primates in Central America	Very high	Increase connectivity; assisted migration; ex situ conservation and reintroduction
High	Low	Low	Primates in the Amazon	Very high	Assisted migration; ex situ conservation and future reintroduction
High	High	Low	Lagomorpha in the western United States	Low to high	Prevention of habitat loss and fragmentation to maintain connectivity for range shifts; potential assisted migration
Low	Low	High	Eulipotyphla in the Appalachian Mountains	Intermediate to high	Increase landscape permeability and connectivity to facilitate range shifts; potential assisted migration
Low	Low	Low	Eulipotyphla in the western United States and Canada	Low to high	Prevention of habitat loss and fragmentation to maintain connectivity for range shifts; potential assisted migration
Low	High	High	Artiodactyla and Xenarthra in eastern Brazil	Low	Increase landscape permeability; nonurgent
Low	High	Low	Carnivora in eastern Canada	Very low	Continue current management practices

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Because rare, long-distance dispersal events can determine the rate of population spread at the edge of a species' range (33), we included the potential for these events in our estimates of dispersal velocity. We used an exponential distribution to describe the variability about the median dispersal distances (12). We multiplied median dispersal distances by the mean of this distribution, which incorporates both the potential for dispersing less than the median dispersal distance and the potential for long-distance dispersal events (Eq. **3**) (12).

Landscape Permeability. To determine the relative degree to which the landscape may impede movement in different regions, we calculated the extent of human-dominated land use that a species would encounter by dispersing from each presently occupied grid cell in a straight line to the closest region of suitable climate. We used the human influence index aggregated to 50 km as a measure of human land use (34). We calculated the length-weighted means of human influence averaged across all species in a given cell and across all climate models.

For a random subset of five species from each of eight orders, we quantified the difference between these straight-line movement paths and dispersal routes that avoid human dominated landscapes and large bodies of water. We compared the velocity species would need to travel to reach suitable climate and the average degree of human land use that species would encounter along these alternative routes. We created least-cost paths from every grid cell in the current range to regions of future suitable climate (*SI Appendix*). Least-cost modeling identifies routes that balance travel through unsuitable landscapes with the additional travel required to avoid less suitable regions (35). We used the human influence index to assign relative costs to movement through each 1-km grid cell (34).

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